Allocation to upper-crown development in reproducing Abies mariesii trees

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論文題目	Allocation to upper-crown development in reproducing *Abies mariesii* trees（繁殖を行っているアオモリトドマツ個体における、樹冠上部の発達への分配について）
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論文内容の要旨

Abstract

Allocation pattern to the crown development of plants is a crucial component to survival, growth, and reproduction in plant life-history traits. Allocation to the development of upper part of tree crown was examined for the individuals of *Abies mariesii* at reproductive stage, and the roles of developing upper part of tree crown were discussed. Two important roles were considered: one is associated with leaf arrangement for effective photosynthesis and the other is with the functional arrangement of reproductive organs. In the process of leaf arrangement, crown expansion acquires space for photosynthetic production. With respect to the direction of the expansion, vertical crown expansion is a process to arrange leaves up to the sunlit space through the competition with the surrounding trees. On the other hand, horizontal crown expansion is a process to increase the amounts of leaves by the acquisition of space for leaf arrangement to avoid the overlapping of leaves. It is more important to allocate photosynthate to vertical than horizontal crown expansion during the competition under the sunlit conditions. For the arrangement of reproductive organs, the location of female reproductive organs is associated with seed dispersal pattern. Several simulation models predict increase in the distance of seed dispersal by wind with increase in the released height of seeds from a seed-producing tree, suggesting that higher location of female reproductive organs is effective to longer seed dispersal. The arrangement of larger amounts of female reproductive organs in higher position needs larger allocation to the upper part of tree crowns. Therefore, the allocation of photosynthate to crown development is related both to competition by height growth and to increasing amount of reproductive organs. Larger allocation at a developmental stage may affect allocation to competition than other stage. To clarify the role of upper part of tree crown at the reproductive stage, the trade-offs between growth and reproduction, and vertical and horizontal growth were elucidated. *A. mariesii* trees develop a crown consisting of a main stem and horizontally elongated branches from the stem. For seed production, seed cones are produced on the branches located in the upper- to middle part of tree crown. I analyzed mainly on the influence of net production and/or reproduction on the expansion of the upper part of tree crown, i.e. the main stem and branches younger than 15 years.

This study consists of three chapters. In the first chapter, the influence of net production per tree on seed-cone production in the upper part of tree crown is discussed by examining the relationship between the cross-sectional area of the main stem at the crown base and the number of seed-cone rachises produced on the primary branches having elongated for 17 years. In the second chapter, specific traits in the allocation trade-off between upper-crown expansion and reproduction in canopy trees is discussed by examining the response of shoot elongation to annually fluctuating seed-cone production and climatic factors. The discussion about the shoot elongation pattern influenced by reproduction is valuable for the understanding of competition and the acquisition of sunlit spaces in reproducing trees. In the third chapter, strategy for intraspecific competition and reproduction in various-sized non-suppressed trees is discussed by

examining growth allocation between height and stem-diameter in each examined year for trees at the reproductive stage.

In the first chapter, seed-cone production in the upper part of tree crown was suggested to increase with net production per tree in various-sized trees but not necessarily increase with net production within large-sized canopy trees. In various-sized trees, there was an allometric relationship between the cross-sectional area of the main stem at the crown base and the number of seed cones in the whole crown. In the relationship, the number of seed cones was proportional to the 1.5 power of the cross-sectional area. Since there were fewer branches producing seed cones in the upper part of tree crown in small-sized trees in comparison with large-sized ones, the allocation to seed-cone production in the upper part of tree crown may increase with increase in net production in a whole tree. On the other hand, within large-sized canopy trees, no relationship was found between the cross-sectional area and the number of seed cones produced in the upper part of tree crown.

In the second chapter, there was a difference between the vertical and horizontal shoot elongation in relations to seed-cone production and/or climatic factors. According to model fitting, for the terminal-leader length of the main stem as the vertical elongation, seed-cone production 1 year before was a negative explanatory variable. On the other hand, for the terminal-leader length of the primary branches as the horizontal shoot elongation, the mean temperature in September 1 year before shoot elongation and the mean temperature in July in the year of shoot elongation were positive explanatory variables. Hence, there may be allocation trade-off between seed-cone production and the height growth, whereas there is not a clear trade-off between seed-cone production and the horizontal crown expansion in the upper part of tree crown.

In the third chapter, the individuals with smaller stem-volume growth showed relatively larger allocation to competition and smaller allocation to reproduction and vice versa in trees with larger growth. In mast years, there were allometric relationships between stem-volume growth and the number of seed cones per tree. In the relationship, the number of seed cones was proportional to the 1.0 to 1.5 power of the stem-volume growth. In the following year of mast seeding, trees with larger stem-volume growth were associated with relatively lower height growth in comparison with trees with smaller stem-volume growth. In various-sized trees, since there is a positive relationship between stem volume and stem-volume growth, findings in this chapter suggest that the allocation of photosynthate to height growth in smaller trees is larger than the allocation in larger trees.

For the role in the upper part of tree crown, findings in this study suggest the smaller allocation to competition and larger allocation to reproduction in trees with larger productivity. On the other hand, within canopy trees, this study suggests that allocation to reproduction in the upper part of tree crown does not necessarily increase with the increase of productivity. In the upper part of tree crown in canopy trees, photosynthate is allocated to both crown expansion and reproduction to ensure the arrangement of needles in the sunlit space by annually fluctuating shoot elongation.

With respect to the role of leaf arrangement, the acquisition of sunlit space by height growth is relatively prominent at the earlier reproductive stage and the efficient utilization of space for photosynthesis by horizontal growth is relatively prominent after the attainment of canopy layer. At the earlier stage, relatively larger growth allocation to height rather than stem diameter may reflect a possibility of competition with surrounding trees. The avoidance of suppression by surrounding trees should be important for survival and the future attainment of canopy layer at this stage. Smaller allocation to reproduction at the earlier stage should be also important for the avoidance of suppression because reproduction affects height growth and might decrease the accumulated photosynthate for needle production. After the attainment of canopy layer, successive allocation to crown expansion may be suitable for polycarpic reproduction in the canopy layer. Successive allocation to the expansion of the upper part of tree crown contributes to the production in the sunlit space and to the future reproduction.

For reproduction in the upper part of tree crown, the allocation to wind seed dispersal increases with increase in the productivity in a tree at the earlier reproductive stage, but does not necessarily increase after the attainment of canopy layer. At the earlier stage, due to increase in both the number and height of seeds released from tree crown, increase in the number of seed cones in the upper part of tree crown with increase in the productivity promotes the function of wind seed dispersal. After the attainment of canopy layer, in the upper part of tree crown, this increase does not occur, being suggested by no relationship between whole-crown size and seed-cone production in the upper part of tree crown within canopy trees. However, in the whole crown, since the number of produced seeds increases with increase in the productivity, the allocation to wind seed dispersal in the whole crown does increase with the productivity.

The role of the upper part of tree crown at the reproductive stage in *A. mariesii* is mainly the attainment of canopy layer and polycarpic reproduction. Polycarpic reproduction in the canopy layer in a long life span is advantageous in relatively stable habitats but is not necessarily effective in habitats frequently experiencing large disturbances. Within relatively stable habitats, since *A. mariesii* canopy trees survive after mast seeding and do not create gaps, successive allocation to crown expansion in the sunlit space may be important to repeat seed production for increasing the chance of recruitment by the seed-producing canopy trees.

This study contributes to the understanding of survival, growth, and reproduction in canopy tree species at the reproductive stage. The findings also help to understand the dynamics of forest canopy consisting of reproducing individuals of canopy tree species.

論文審査結果の要旨

植物の栄養成長と繁殖成長への分配トレードオフは，その種の生活史戦略上重要な意味をもつ。とくに，樹木では樹冠上部での物質分配様式の役割が大きい。樹冠拡大は光合成生産に必要な空間を獲得する役割をもつが，垂直方向の樹冠拡大が周辺の個体との競争を通じて光条件の好適な空間に葉を配置する過程であるのに対して、水平方向の樹冠拡大は、葉の重なりを回避するために葉の配置に適した空間の獲得によって葉量を増大する過程であり，この二つの戦略も関係する。一方，樹木の発達段階にともなって，これらのトレードオフ関係が変化することも予想される。学位申請者関剛氏の研究は，繁殖と成長のトレードオフを前提に，垂直方向と水平方向の樹冠成長の間の分配もあわせて解析したものである。

第一章では、樹冠上部における球果生産が、個体あたり純生産の増大にともなって増大するが、林冠層に達した大きいサイズの個体では必ずしも増大しないことが示唆された。繁殖開始後の若い個体では個体あたりの純生産の増大にともなって増加することが示された。

第二章では、垂直方向の伸長としての主幹当年伸長量に対し、伸長 1 年前の球果生産が負の影響を持つことが明らかとなった。水平方向の伸長には球果生産の影響がないものの、伸長前年 9 月の平均気温と伸長当年 7 月の平均気温が正の効果をもっていた。したがって、球果生産は主として樹高成長とトレード・オフが大きいことが明らかとなった。

第三章では、主幹の体積成長の樹高・肥大成長への配分と種子生産の関係を扱い，成長量の小さい個体ほど競争に対して相対的に高い分配を示し、繁殖に対して低い分配を持つことを明らかにした。種子豊作年には、主幹体積成長量成長量の大きい個体では相対的に翌年の樹高成長が低かったが，肥大成長には大きな影響がなかった。また，よりサイズの小さい個体では，樹高成長への光合成産物の分配がサイズの大きい個体に比べて大きいことが示唆された。

この研究は，樹木の繁殖と成長のトレードオフが，主として樹高成長に効いていること，さらに垂直・水平方向への樹冠拡大の生活史段階とともにその関係が変化すること，さらにその変化に，年次変動の大きい繁殖が関与することを示した点で新しい知見であり，寿命の長い樹木の生活史スケジュールおよびその戦略を探る上で，新しいアプローチと言える。一連の研究とその成果は，自立して研究活動を行うに必要な高度の研究能力と学識を有することを示している。したがって，関剛氏提出の論文は，博士（生命科学）の博士論文として合格と認める。